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Age Differences in Behavioral Responses of Male Giant Pandas to Chemosensory Stimulation

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Abstract: Chemical communication plays an important role in survival and reproductive success in mammalian species. In the present study, we examined the ontogenetic pattern of behavioral responses of male giant pandas (*Ailuropoda melanoleuca*) to urine odors of conspecific individuals. Our data showed that exposure to the urine of adult females induced a significant increase in sniffing and environmental sniffing/licking behaviors, but a decrease in biting behavior, in males. Males of different ages displayed specific behaviors to female urine odors. Adult males spent more time licking than juvenile and sub-adult males. Further, sub-adult and adult males displayed high levels of environmental sniffing/licking, which was absent in the juvenile males. Juvenile males displayed scent rubbing behavior significantly more frequently than sub-adult and adult males, and also spent more time showing biting behavior than sub-adult males. Finally, juvenile and sub-adult males showed no difference in response to female and male urine odors. Together, these data suggest that chemosensory cues from conspecific urines induce age-specific responses in male giant pandas.

Key words: Giant panda; Urine odor; Chemical communication; Behavioral development

雄性大熊猫对化学信息行为反应的年龄差异

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摘要: 化学通讯对哺乳动物的生存和繁殖起着重要作用。研究了雄性大熊猫(*Ailuropoda melanoleuca*)对同伴个体尿液气味行为反应的发育模式。结果显示, 在成年雌性个体的尿液气味刺激下, 雄性个体表现显著多的嗅闻行为和嗅闻/舔舐环境行为, 但是嘶咬气味刺激物的行为明显减少。在雌性个体的尿液气味刺激下, 不同年龄段的雄性个体行为表现不同, 成年雄性个体表现较亚成年和幼年个体显著多的舔舐行为。此外, 成年个体和亚成年个体均表现较多的嗅闻/舔舐环境行为, 而幼年个体则无该行为表现。幼年个体较成年和亚成年个体表现显著多的气味涂抹行为, 而且嘶咬气味刺激物的时间较亚成年个体显著多。幼年个体和亚成年个体对雌性和雄性个体尿液气味刺激的行为反应不存在显著差异。研究结果表明, 雄性大熊猫对同种个体尿液中化学信息的行为反应呈现出年龄差异。

关键词: 大熊猫; 尿液气味; 化学通讯; 行为发育
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Chemical communication plays an important role in locating potential mates, maintaining social struc-

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tures, and promoting reproductive success among mammalian species (Conover & Gittleman, 1989; Johnston, 1990; Hurst & Rich, 1999; Johnston, 1999; Müller-Schwarze, 1999). The majority of research on the behavioral effects of chemical communication has been conducted in small rodents (Johnston, 1979; Holmes & Sherman, 1982; Dorries, 1999). Recently, studies have also been carried out on large, rare species of mammals (Alberts, 1999; Rasmussen & Schulte, 1999; Salamon et al, 1999; Swaisgood et al, 1999; Swaisgood et al, 2000; Liu et al, 2005).

Giant pandas are a solitary species in the wild, and they communicate with each other by 'scent-mark stations', on which odors from bodies, urine and anogenital gland secretions are deposited (Hu et al, 1985; Pan et al, 2001). In captivity, adult pandas often leave scents on the ground, walls, and projecting surfaces. Using multiple chemical cues (urine, feces and anogenital gland secretions) they can discriminate the sex and reproductive conditions of the donors (Swaisgood et al, 2000). Both adult and sub-adult pandas can discriminate age differences of the donors via odors emanating from male urine, male anogenital gland secretions and female urine, showing a pronounced preference for adult odors (White et al, 2003). It has been reported that marking and chemosensory investigation behaviors differ between male and female adult pandas, and that these behaviors are influenced by individual reproductive conditions (Liu et al, 2002; White et al, 2003). However, little is known about the developmental pattern of chemical investigation behaviors in giant pandas. If the developmental pattern of chemical investigation behaviors shows the same pattern as physiological development, we can predict that adult male pandas should display much more sniffing of the female conspecifics urine odor and show correlations with age. To test the above prediction, the present study was therefore designed to examine the behavioral responses of male giant pandas to the urine odors from adult conspecifics. We compared the behavior of juvenile, sub-adult and adult male pandas to reveal the characteristics and development profiles of behaviors related to chemical communication.

1 Materials and Methods

1.1 Subjects

The subjects were male giant pandas ($n = 10$) that were housed in the China Conservation and Research Center for the Giant Panda (CCRCGP), Wolong Nature Reserve, Sichuan Province, China. Field studies on giant pandas show that cubs are usually weaned at 8 – 9 months of age and continue to live with their mothers until approximately 1.5 years old. After 1.5 years old, young pandas may live independently and at the age of three they start to set up their territories that overlap with their mothers' (Hu et al, 1985; Pan et al, 2001). Male pandas sexually maturate and establish their own territories at approximately 4.5 years of age (Hu et al, 1985; Pan et al, 2001). Accordingly, in the present study, 10 subjects were assigned into the juvenile group (1.5 years old or younger, $n = 3$), sub-adult group (1.5 – 4.5 years old, $n = 3$), and adult group (older than 5 years, $n = 4$), respectively.

Subjects were housed individually in an enclosure containing an indoor pen (5.8 m × 2.3 m) and an outdoor yard (5.8 m × 13 m) with grass, climbing apparatus, and a small pond as a water source. Each outdoor enclosure adjoined two others via a cement wall, in which there was a small wire-mesh door (0.5 m × 9 m). Therefore, subjects could see, smell, hear and have limited physical contact through the mesh fence, with neighboring animals. Management regimes for the giant pandas have! been described previously (Liu et al, 1998).

1.2 Urine collection

This research was carried out during the mating season (April to June) of 2002. Male and oestrous female pandas make scent marks by excreting a small or large quantity of urine (Hu et al, 1985; Hu, 1990). Therefore, urine of adult pandas (donors) was collected as chemical stimuli. Adult females that had no mating experience in 2002 and sexually active adult males were chosen as donors. To avoid possible effects of kin relationship and familiarity on behavior, close relatives (siblings, parents or offspring) and neighbors of the subjects were not used as donors. Previous evidence indicates that female reproductive status effects the discrimination test (Swaisgood et al, 2000). Therefore we chose oestrous females that were not yet in a receptive state (heat time) as our urine donors. Fresh urine samples were collected with a syringe from the concrete surface of the pen and then stored at −20℃ 10 to 20 days before the test. A new syringe was used for each sample collection. In total, we used four adult females (studbook numbers: 385, 414, 446 and 544) meeting the above criteria of genetic relationship and reproduc-

tive status as female urine donors. We also used three adult males (studbook numbers: 329, 399 and 413) as male urine donors for the sub-adult and juvenile pandas.

1.3 Experimental design

Subjects were exposed to female urine or controls. Frozen urine was taken out of a refrigerator 30 min before each experiment. The urine sample was provided by using a piece of gauze (40 cm × 32 cm) that was folded to a slice and soaked with 10 mL of donor urine. A similar size of gauze without urine was used as the control sample. Further, in the juvenile and sub-adult groups, subjects were also exposed to the male urine odors. This treatment was not applied to the adult male subjects due to consideration of potential inhibitory effects of male chemosensory cues on the subject's reproductive physiology and behavior. The sample was put in the indoor pen near the subject. Behavioral tape recording started at the time when a subject showed the first obvious response to the sample (sniffing or touching) and the recording lasted 10 min. Feeding time was avoided in the experiments. Each subject was exposed to a sample containing urine from one donor or to the control sample on each trial. The order of urine exposure (control, female or male urine) was carried out randomly to prevent the subjects' memory for the odors. The control tests for each subject were repeated three times. Each subject was tested using the odors from two donors and three test trials were run using the odor of each donor. There was at least a one-day interval between trials.

The videotapes were later replayed, and the duration of the following behaviors in each trial was recorded using a digital timer (Model MC No.4450 – 110, made by Feiyada Company) with focal sampling and continuously recording method (Martin & Bateson, 1986). Behavioral patterns directed to the urine sample include sniffing: investigating the sample with the nose at a distance of less than 5 cm; licking: touching the sample with the tongue (the bout criterion interval is 2 seconds); touching: contacting the sample with paws (sniffing or licking was recorded if touching was displayed simultaneously with sniffing or licking); scent rubbing: picking up the sample with the paws and rubbing it over the arm, head, neck or abdomen; and biting: chewing or biting into the sample and often tearing the sample with the paws. One additional behavioral pattern was also recorded: environmental sniffing/licking: sniffing or licking objects or places in the enclosure other than the urine sample (sniffing/licking elicited by food was excluded). The frequency of scent marking: rubbing the anogenital area around or up and down on the wall, ground or other surface or urinating or defecating on the wall or ground in all postures; was also recorded. Similar behavioral categories were used in previous studies (Liu et al, 1998; White et al, 2002; Liu et al, 2003).

1.4 Data Analysis

Data from different trials were combined for each subject, and the mean of each behavior was used for analysis. To test the treatment effects of female urine on the male's behavior, the behavioral responses of male pandas to the control and the urine odor of female donors were analyzed using Wilcoxon signed ranks test regardless of age differences. Age differences in behavioral responses of males to the female urine odors were analyzed using Kruskal-Wallis tests followed by Mann-Whitney U tests. In addition, changes of behavioral patterns during development were examined using the Spearman correlation coefficient. The correlation between the duration of each behavioral category and the ages of the subjects by year and experimental group (experiment or control) were assessed regardless of their age group differences. For the juvenile and sub-adult groups, subjects' behavioral responses to the different chemosensory stimuli (control, female or male urine) were analyzed using a Friedman test followed by a Wilcoxon Signed Ranks test. The age was rounded up to 0.5 years. The level of significance was set to 0.05. All tests were two tailed.

2 Results

Exposure to the urine from oestrous females altered the behavior of male recipients. Males, with all age groups included, showed a significant increase in the duration of sniffing (Wilcoxon $Z = -2.599$, $n = 10$, $P < 0.05$) and environmental sniffing/licking ($Z = -2.366$; $n = 10$, $P < 0.05$), but a decrease in biting behavior ($Z = -2.380$; $n = 10$, $P < 0.05$) when exposed to the female urine compared with the control (Fig. 1). No treatment effects were found in other observed behavioral patterns. When analyzed separately, none of the three groups responded to female urine odors significantly differently from the control (Tab. 1).

The behavioral patterns of males to female urine

Tab. 1　Behavioral responses of male giant pandas to urine odor of adult female conspecifics

	Juvenile		Sub-adult		Adult	
	Control	Female	Control	Female	Control	Female
Sniffing	2.8 ± 1.9*	26.0 ± 11.5	8.0 ± 0.1	11.2 ± 3.1	7.7 ± 2.1	28.1 ± 10.5
Licking	1.7 ± 1.7	1.0 ± 1.0	0	0.9 ± 0.5	0	45.0 ± 22.4
Touching	4.2 ± 2.1	5.2 ± 2.6	0.1 ± 0.1	17.1 ± 16.2	2.8 ± 1.9	1.9 ± 0.8
Biting	136.3 ± 83.4	22.7 ± 11.7	47.3 ± 14.8	0	13.5 ± 13.5	3.2 ± 3.0
Scent rubbing	0	3.9 ± 1.7	0.1 ± 0.1	0	0	0
Environ-Sniffing	0	0	0.9 ± 0.9	18.3 ± 6.4	1.8 ± 0.7	18.0 ± 5.3

* Mean ± *SE* in sec.

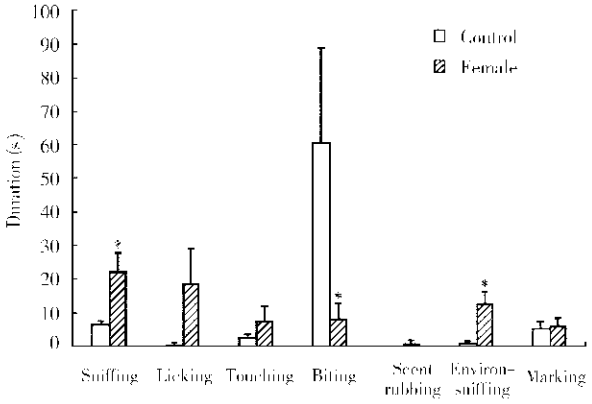

Fig. 1　Effects of exposure to urine odor from conspecific adult females significantly altered behaviors of male giant pandas
* $P < 0.05$.

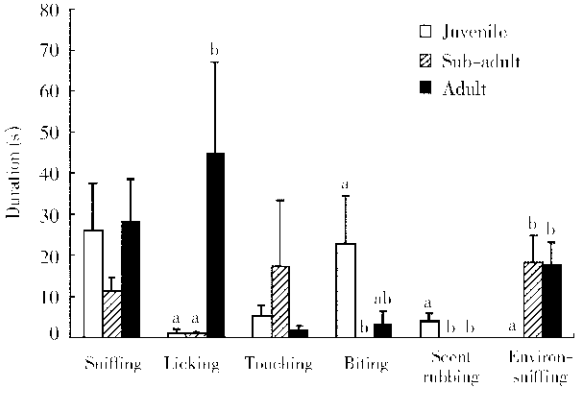

Fig. 2　Age effect on behavioral response of male giant pandas to urine odor from conspecific females
The alphabetic letters indicated group differences illustrated by Mann-Whitney *U* tests. Groups with the same letter did not differ from each other.

were affected by age. When exposed to controls, only one significant difference was found between different age groups. Adult males displayed scent marking behavior more frequently than sub-adult (Mann-Whitney $U = 0.00$, $P < 0.05$) and juvenile males (Mann-Whitney $U = 0.00$, $P < 0.05$). However, when exposed to female urine, several behavioral age-differences were found. Adult males spent more time licking than juvenile and sub-adult males (Mann-Whitney $U = 0.00$, $P < 0.05$). Sub-adult and adult males displayed similar levels of environmental sniffing/licking, which was absent in the juvenile males. On the other hand, juvenile males displayed scent rubbing behavior significantly more frequently and spent more time biting than sub-adult males did (for rubbing, Mann-Whitney $U = 0.00$, $P < 0.05$; for biting, $U = 0.00$, $P < 0.05$) (Fig. 2). During exposure to female urine, a significant increase in licking behavior ($n = 10$, $r = 0.77$, $P < 0.05$) and a significant decrease in scent rubbing behavior ($n = 10$, $r = -0.81$, $P < 0.05$) over ages were also found. Finally, when being exposed to the clean gauze (control), a significant increase in the duration of stereotyped behavior ($n = 10$, $r = 0.77$, $P < 0.05$) and in the frequeny of scent marking ($n = 10$, $r = 0.90$, $P < 0.05$) was found over age, whereas the duration of biting behavior showed a significant decrease ($n = 10$, $r = -0.64$, $P < 0.05$) over age.

Juvenile and sub-adult subjects were also exposed to male urine. Our data indicated that exposure to male or female urine induced a similar increase in the sniffing behavior (Friedman test, $\chi^2 = 7.00$, $df = 2$, $P < 0.05$) but a decrease in biting behavior (Friedman test, $\chi^2 = 10.17$, $df = 2$, $P < 0.01$) (Fig. 3). No significant difference was found between the behavioral responses of juvenile and sub-adult males to adult male urine odors and female urine odors. No treatment effects were found when juvenile and sub-adult males were analyzed separately.

3　Discussion

Chemical communication plays an important role in regulating physiological and behavioral functions in animals, such as identification of potential mates, induction and/or synchronization of oestrus, and successful

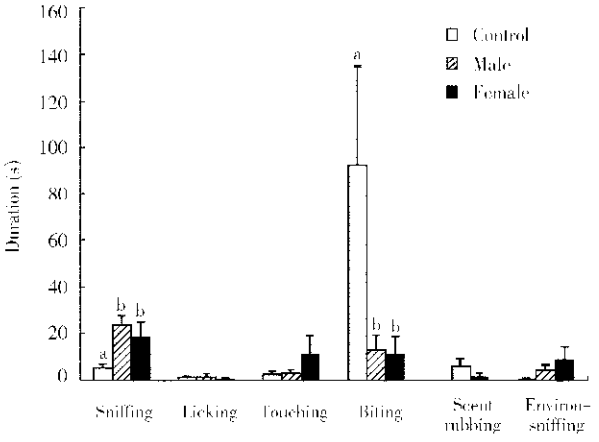

Fig. 3 Behaviors of juvenile and sub-adult male pandas in responding to urine odor from either male or female conspecifics

The alphabetic letters indicate group differences illustrated by Wilcoxon Signed Ranks tests. Groups with the same letter did not differ from each other.

completion of mating (Floody et al, 1977; Johnston, 1979). Urine usually contains information regarding the donors' identity, including sex, endocrine condition and social status, and thus serves as an important channel for chemical communication in a variety of mammalian species including the giant panda (Hu et al, 1985; Swaisgood et al, 1999; White et al, 2002; White et al, 2003). Our data not only confirmed that male giant pandas responded behaviorally to urine odors from conspecific individuals, but also demonstrated that such responses were age-dependent.

In our study, exposure to urine odor from a conspecific oestrous female induced a significant increase in sniffing and environmental sniffing/licking behaviors, and a decrease in biting behavior, in male giant pandas. These data further confirmed the previous findings that urine odors induced changes in male giant panda behavior (Swaisgood et al, 1999). In addition, it is interesting to note that in our experiment, sniffing or licking behavior was often followed by environmental sniffing/licking behavior. After investigating urine samples from conspecifics, male giant pandas usually sniffed and/or licked their own urine/feces or the places where they or the former residents deposited the scent previously. These findings suggest that male pandas may examine whether the donor has marked over its urine on their own 'scent-mark stations' (Johnston & Chiang, 1994; Johnston, 1999), or they may discriminate between the urine cue from a conspecific individual and their own odors (Heth et al, 1998; Mateo & Johnston, 2000).

Another important finding in the present study is the developmental profile of male giant panda behavior. The changes of particular behaviors at certain ages are related to physiological differences and may indicate a functional significance of the behavior. For example, scent marking is mediated by hormones from the pituitary, gonads and thyroid (Edling, 1977; Johnston, 1981), and is an important behavior for advertising one's identity and defending its territory from conspecific intruders (Conover & Gittleman, 1989; Johnston, 1999; Müller-Schwarze, 1999). Our results showed that juvenile pandas did not display scent marking until they are mature, whereas adult males had well-developed scent marking behavior, and the frequency of scent marking increased over age under control conditions. Juveniles might lack a mature physiological basis for scent marking. Interestingly, biting behavior and scent rubbing were predominantly displayed by juveniles. Moreover, these two behaviors were lacking when tested with unscented gauze (control), and were also rarely seen in sub-adult and adult males. We speculated that biting behavior seen in juveniles might belong to the category of playing behavior-object playing (Fagen, 1981; Thompson, 1998). Younger pandas display more playing behavior than older ones in captivity (Liu et al, 2002). Our results in playing behavior are consistent with Liu et al (2002). The function and application of playing behaviors are: 1) to practice the behavior which may be used as an adult; and 2) to provide information concerning the environment and an individual's abilities and limitations (Bunnell, 1986). Younger pandas display more object playing behavior, which might be helpful in learning to manipulate bamboo as an adult. The underlying mechanism of age differences in scent rubbing behavior, however, was complicated and may req uire further research in the future. Previous evidence indicates that younger pandas face a higher pressure of predation or aggression than older pandas (Wei et al, 1990), and younger pandas are often seen playing or staying in the tree in the wild (Pan et al, 2001). Although juveniles usually picked up the scented gauze and then smeared it on their body surface, they rarely display scent rubbing with clean gauze. Evidence shows that protective mimicry commonly exists in insects, some amphibians, reptiles and birds (Brown,

1879), yet no evidence is available in mammals. Therefore, we conservatively speculated that the scent rubbing behavior in juveniles was also a kind of playing behavior, in the absence of sound evidence of protective mimicry.

Finally, the drawback in our study was the limited number of available subjects, which likely has prevented us from detecting some significant effects. Nevertheless, our data indicates that male giant pandas at different developmental stages responded to urine cues from conspecifics in a behavior- and stimulus-specific manner. Further studies are needed to understand the functional significance of behavior changes during development and in response to urine cues, which in turn, may provide useful information for management and breeding of captive giant pandas.

4 Conclusion

Exposure to adult female urine odors induced a significant increase in assessing behavior in male pandas, and the chemosensory cues from conspecific urine induce age-dependent responses in male giant pandas.

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2006 年《动物学研究》编辑部收稿 413 篇，其中英文稿件 58 篇；英文稿件中，国外来稿 25 篇。同年刊发论文 95 篇，其中英文论文 23 篇，比去年增加 9 篇，占全部发表论文的 24%。2007 年本刊在中国国际图书贸易公司的发行数量较过去有明显提高。可喜的是，2006 年本刊在云南省新闻出版局举办的云南省第二届优秀期刊评选活动中获得了最高奖励——优秀期刊奖。这些成绩与作者和审稿人的鼎力支持密不可分。为此，我们对曾向本刊投稿的作者致以诚挚的感谢！对审稿人为本刊付出的心血表示崇高的敬意！为表达我们由衷的感激之情，现以姓氏拼音为序，列出 2006 年度的审稿人。

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